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Grazing preference of *Onychiurus subtenuis* (Collembola) and *Oppiella nova* (Oribatei) for fungal species inoculated on pine needles

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Summary. Feeding preference on litter fungi of two sympatric microarthropods, *Onychiurus subtenuis* Folsom (Collembola) and *Oppiella nova* (Oudemans) (oribatid mite) was compared by a laboratory choice test. Nine most frequently observed litter fungi from a lodgepole pine forest in the Kananaskis Valley in SW Alberta, Canada, were served for the test. Both animal species showed consistent preference order on the test fungi, and two animal species had similar preference order on the test fungi. *O. subtenuis* showed different preference order on agar-grown fungi and litter-grown fungi, although *O. nova* did not change their preference. Both species showed significant preference on the fungi with thicker diameter of hyphae grown on agar, although the preference was not correlated to the fungi grown on needle. The mortality of the both animals reared on the single test fungi were worst when the least preferred fungi was served as a food but was not significantly different for other test fungi.

Key words: Collembola, feeding preference, fungal feeding, *Onychiurus subtenuis*, *Oppiella nova*, oribatid mites

Introduction

Collembola and oribatid mites are the dominant arthropods in many soils (Petersen & Luxton 1982). The feeding habits of these animals have been studied using field observation and laboratory tests. Fungal grazing by Collembola and oribatid mites has been confirmed by gut content analysis of field populations (Anderson & Healy 1972; Behan & Hill 1978; McMillan 1976; Mitchell & Parkinson 1976; Poole 1959). Collembolan species tend to show indiscriminate feeding habits in the field (Addison 1977; Anderson & Healy 1972; McMillan 1975; Takeda & Ichimura 1983; Poole 1959), e.g. their guts contain both fungal and higher plant materials as well as mineral soil particles. Compared to Collembola, oribatid mites have distinct feeding preferences (Hartenstein 1962; Luxton 1972) even in the field (Kaneko 1988) and are classified as macrophytophagous (higher plant debris feeders), microphytophagous (microbial feeders) or panphytophagous (indiscriminate saprotrophic feeders) (Luxton 1972). Although Behan-Pelletier and Hill (1983) classified most oribatid mites found in a moorland bog as panphytophagous, fungal materials were almost always associated with plant matter in gut contents.

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Laboratory feeding choice tests have demonstrated strong preferences for different fungal species by Collembola (Klironomos et al. 1992; McMillan 1976; Moore et al. 1987; Schultz 1991; Shaw 1988; Visser & Whitakker 1977) and oribatid mites (Hartenstein 1962; Luxton 1972; Mitchell & Parkinson 1976; Stefaniak and Seniczak 1981). Microarthropod choice of fungal species was influenced by fungal colony age (Moore et al. 1987; Saichuae 1972), nutrient status of fungal medium (Booth & Anderson 1979; Leonard 1984) and probably toxic fungal metabolites (Visser & Whitakker 1977) as well as fungal species. Odour appears to be a useful key for fungal choice by soil microarthropods (Bengtsson et al. 1988; Bengtsson et al. 1991).

In most preference tests fungi have been grown on agar, even ectomycorrhizal species (McMillan 1976; Mueller et al. 1990; Shaw 1988). However, preference is affected by the substrate on which test fungi are grown (Klironomos et al. 1992; Leonard 1984) and this appears to be related to the changes in fungal volatiles (Bengtsson et al. 1988; Bengtsson et al. 1991). Some Phthiracarid mite species were shown to prefer needles at certain stages of decomposition, although fungal species on the needles were not identified (Hayes 1963). If the substrate quality affects fungal growth and chemistry, previously demonstrated differences in fungal preference may not reflect natural conditions.

Natural litter contains many species of fungi and selective feeding by soil animals may change interactions between fungal species (Parkinson et al. 1979; Newell 1984a, b). In Lodgepole pine forest soils in the Kananaskis Valley in SW Alberta, Canada the most common species of Collembola and oribatid mite are *Onychiurus subtenuis* Folsom and *Oppiella nova* (Oudemans), respectively, and as fungivores are potential competitors for litter fungi. Selective feeding of fungi by soil animals is important since if the fungal species has different toxic and nutritional effects on animals, fungal food may affects reproductive success and survival of animal populations (Amelsvoort et al. 1989; Stefaniak & Seniczak 1981).

There are no studies comparing feeding preference of sympatric Collembola and oribatid mites. This experiment was designed to answer the following questions: 1) do *O. subtenuis* and *O. nova* have consistent preferences for common pine needle litter fungi? 2) do these two animals prefer the same fungi? 3) do these preferences differ when the fungi are grown on agar or needles? 4) do the preferences correlate to the animal's survival on that fungus?

Materials and Methods

Fungi

Fungal species used for the test were isolated from natural litter in a lodgepole pine forest of the Kananaskis Valley in the Rocky Mountains of Alberta. Needle litter was collected on February 27, 1992 from the forest floor. Needles were kept moist at 5 °C for one month, then soaked for one day in deionized water to obtain uniform water contents.

Needles were placed in a 135 ml jar with five sheets of glass fiber filter on the bottom. One ml deionized water was added to the filters and the jars were incubated for one week at 15 °C. Fungi present as spores were removed using a litter washing technique (Parkinson 1982) to determine fungi present as actively growing hyphae. Needle pieces were washed in 15 changes of water (determined by preliminary experiment), placed on sterile filter paper to remove excess water, aseptically cut into 1 mm particles and one particle placed on each plate. From each of four replicates, 30 particles were plated on 2% malt extract agar plus antibiotics (0.01% streptomycin and 0.005% chlortetracycline hydrochloride) to inhibit bacterial growth, and 20 particles were plated on 2% malt extract agar with antibiotics (as above) plus 0.0005% benomyl to isolate basidiomycetes (Worrall 1991).

Fungi growing on the plates were isolated onto 2% malt extract agar at two weeks. The 12 most common species present in pure culture were tested for their ability to grow on needles.

Inoculation test

Pine needles collected from the same site in fall 1991, and stored in plastic bags at 5 °C were used in this experiment. The needles were cut into 1 cm pieces, soaked in water for 48 hours and excess water drained off. A single layer of needles (1 g dry weight) was placed in the bottom of glass petri plates which had moistened asbestos rope around the inside wall to maintain moisture content. The petri plates were then autoclaved at 15 psi for 20 minutes to kill all fungi and bacteria present on the needles. Each petri plate of autoclaved needles was inoculated with one of the 12 most commonly isolated species of fungi discussed above. Four pieces (0.5 by 0.5 cm) of agar were cut from the growing edge of each pure culture of fungus, transferred onto the needles, and incubated for two to three weeks. Nine fungi growing evenly and densely on the needles were chosen for use in the preference and mortality test (Table 1).

Table 1. Fungal taxa used in the preference test and their rank (frequency of occurrence) on the initial isolation plates and hyphal diameter

Taxon	Rank	Hyphal diameter (μm)		
		low	high	median
Sterile dark 516	1	1.2	12.0	6.6
Phoma 445	2	1.2	3.6	2.4
cf *Microstroma* 443	3	1.2	5.0	3.1
cf *Microstroma* 449	4	1.2	6.0	3.6
Sterile dark 517	5	2.4	25.0	13.7
Cladosporium herbarum	6	1.4	5.0	3.2
Sterile dark 487	7	1.0	6.0	3.5
Aureobasidium pullulans	8	1.2	7.2	4.2
Basidiomycete 498	9	1.8	2.4	2.1

Fauna

Soil blocks were collected from the forest site and animals extracted using a Tullgren funnel one week before the experiment began. *Onychiurus subtenuis* and *Oppiella nova* were picked up using a fine brush, placed in jars containing a plaster and charcoal mixture moistened to maintain humidity and held at 15 °C in the dark. The animals were fed baker's yeast then starved for two days before introduction to the test jars. Jars were maintained at 15 °C in the dark.

Experimental design

The preference of *O. subtenuis* and *O. nova* for each of nine species of fungi grown on agar was tested. The two species of animals were tested separately and the fungi were presented in pairs along with a control (MEA) to determine a preference ranking between all nine species of fungi. All 36 combinations were tested and each pairwise comparison was replicated four times.

The test was conducted in flat wall glass jars (6 cm height by 5.5 cm inside diameter) with 2 cm of Plaster of Paris on the bottom to maintain humidity. Disks of agar 0.5 cm in diameter were cut from the growing edge of the fungal colonies and placed in a circle on the plaster with pairs of fungal disks opposite each other (i.e. fungus A, fungus B, control, fungus A, fungus B, control in order). Two fungal species and control disks of MEA were used in each case. Five Collembola or ten oribatid mites were introduced to each test jar and the number of animals found on each agar disk was recorded 24 hours after the introduction of the animals to the jars.

The preference of *O. subtenuis* and *O. nova* for each of nine species of fungi inoculated onto autoclaved needles was tested using the same experimental design as above. This test was conducted in flat wall glass jars (6 cm height by 5.5 cm inside diameter) with 2 cm of Plaster of Paris on the bottom. Just before the beginning of the experiment, a thin layer of plaster was added to the jar and the inoculated needles were set into the surface before it hardened to reduce the possibility that animals would be attracted to the needles merely as shelter. In each jar, six needles were placed radially with pairs of needles opposite each other. Two needles were autoclaved needles, or controls, and two needles of each of two species of fungi were used. Five *O. subtenuis* or ten *O. nova* were introduced to each test jar and the number of animals found on each needle was recorded 24 hours after the introduction of the animals to the jars.

To determine if the animals could survive on each of the nine test species of fungi, seven Collembola or 20 mites were tested separately in jars containing needles inoculated with each of the nine fungal species. Each treatment was replicated four times. Test fungi were inoculated onto 1 cm pieces of autoclaved pine needles. After the fungi had grown, 0.3 g (fresh weight) needles were placed in each jar. Autoclaved needles were used as a control. Jars were kept at 15 °C in the dark. Surviving animals were counted after 4 weeks.

For each fungal taxon, the range of fungal hyphal diameters were measured at 440 × magnification.

Statistics

Feeding choice data was analyzed using the student's t-test and a rank table was constructed using significant differences. Percentage mortality data was arc-sin transformed and then analyzed using 1- and 2-way ANOVA. Spearman's coefficient of rank correlation was used to determine whether each species' ranked preference of fungi on agar and needles differed and whether there were significant differences between the preferences of *O. subtenuis* and *O. nova*.

Results

Although MEA or needles were offered as a choice in all the pairwise comparisons, there was no evidence of faunal interest in these as a food and in all cases, fungi were preferred to the control.

Fungal species preferred by each animal are ranked in Tables 2 and 3. Some fungi were obviously preferred, although due to high variability among replicates, there was no

Table 2. Derivation of the palatability ranking for *O. subtenuis*

Fungal taxon	Number of fungi significantly less preferred	Number of fungi significantly more preferred	a − b	rank
O. subtenuis-agar				
Sterile dark 516	4	0	4	1
cf *Microstroma* 449	4	0	4	1
Sterile dark 517	4	0	4	1
Cladosporium herbarum	3	1	2	4
cf *Microstroma* 443	3	1	2	4
Aureobasidium pullulans	3	2	1	6
Sterile dark sp 487	1	5	−4	7
Basidiomycete 498	0	6	−6	8
Phoma 445	0	7	−7	9
O. subtenuis-needle				
Cladosporium herbarum	4	0	4	1
Sterile dark 517	3	0	3	2
Sterile dark 516	2	0	2	3
Phoma sp 445	1	1	0	4
cf *Microstroma* 449	0	0	0	4
Aureobasidium pullulans	1	2	−1	6
Sterile dark 487	0	2	−2	7
cf *Microstroma* 443	0	3	−3	7
Basidiomycete 498	0	3	−3	9

Table 3. Derivation of the palatability ranking for *O. nova*

Fungal taxon	Number of fungi significantly less preferred	Number of fungi significantly more preferred	a − b	rank
O. nova-agar				
Cladosporium herbarum	6	0	6	1
Sterile dark 517	5	1	4	2
Sterile dark 516	3	0	3	3
Aureobasidium pullulans	2	1	1	4
Sterile dark 487	1	2	−1	5
cf *Microstroma* 449	1	2	−1	5
Basidiomycete 498	1	4	−3	7
cf *Microstroma* 443	1	4	−3	8
Phoma 445	0	6	−6	9
O. nova-needle				
Cladosporium herbarum	4	0	4	1
Sterile dark 487	4	0	4	1
Sterile dark 517	3	1	2	3
Sterile dark 516	2	3	−1	4
Phoma 445	1	2	−1	4
cf *Microstroma* 449	0	1	−1	4
Aureobasidium pullulans	0	1	−1	4
Basidiomycete 498	1	3	−2	8
cf *Microstroma* 443	0	4	−4	9

significant difference in preference between many pairs. Out of 36 combinations, only 22, 11, 20 and 15 pairs were significantly different ($p < 0.05$) for *O. subtenuis*/agar, *O. subtenuis*/needle, *O. nova*/agar and *O. nova*/needle, respectively.

There were clear preferences shown by both animal species (Tables 2 and 3). For both animals, *Cladosporium herbarum*, Sterile dark 517 and Sterile dark 516 were among the four most preferred fungi on needles and agar. For both animals, cf *Microstroma* 443 and Basidiomycete 498 were the least preferred fungi on needles. *Phoma* 445 was least preferred on agar.

There was a significant correlation between Collembola and mite preferences for fungi grown on needles ($\varrho = 0.644$, $p < 0.05$), and a significant correlation between Collembola and mite preferences for fungi grown on agar ($\varrho = 0.615$, $p < 0.05$). For *O. subtenuis* fungal preference for fungi growing on agar and needles was not significantly correlated ($\varrho = 0.519$) however, for *O. nova* it was significantly correlated ($\varrho = 0.650$, $p < 0.059$). The preferences on the fungi grown on agar were significantly correlated to increasing hyphal diameter for *O. subtenuis* ($\varrho = 0.717$, $P < 0.05$) and for *O. nova* ($\varrho = 0.714$, $P < 0.05$), although it were not significantly correlated in the case of needle-grown fungi for *O. subtenuis* ($\varrho = 0.552$) and *O. nova* ($\varrho = 0.402$). Sterile dark species, Sterile dark 516, and 517 had thicker hyphal diameter and were preferred in the agar test, whereas, Basidiomycete 498 and *Phoma* 445 were the thinnest and were denied in the agar test. In the needle test, these relationships were not obvious.

Mortality of *O. subtenuis* and *O. nova* differed depending on fungal species, and animal × fungal interaction was also shown (Table 4). Mean mortality ranged from 2 to 98% and from 17 to 82% for *O. subtenuis* and *O. nova*, respectively. *O. subtenuis* showed 98% mortality in the presence of cf *Microstroma* 443, while in the presence of the control, with no fungi, showed 78% mortality (Table 5). Similar results were obtained for *O. nova*, with the control causing the highest mortality (82%) and cf *Microstroma* 443 causing 50%

Table 4. Analysis of variance of mortality data for *O. subtenuis* and *O. nova*

Source of Variance	d.f.	F ratios
animal	1	8.924**
fungal taxon	9	17.189**
animal × fungal taxon	9	4.761**
residual	60	

** significant at $P < 0.01$

Table 5. Mean percent mortality of *O. subtenuis* and *O. nova* when fed only one fungal taxon growing on needles. Data arc-sin transformed for ANOVA and backtransformed for the table. Values within columns followed by the same letter are not significantly different (LSD). For *O. subtenuis*, F10, 33 = 14.23** and for *O. nova*, F10, 33 = 8.95**

O. subtenuis		*O. nova*	
Fungal taxon	mortality (%)	Fungal taxon	mortality (%)
cf *Microstroma* 443	98.0a	Control	81.8a
Control	70.8b	cf *Microstroma* 443	50.0b
Sterile dark 487	21.0c	cf *Microstroma* 449	34.7c
Basidiomycete 498	17.5c	Sterile dark 487	33.6c
Sterile dark 517	17.5c	*Cladosporium herbarum*	31.2c
cf *Microstroma* 449	13.2c	Basidiomycete 498	30.9c
Phoma 445	13.2c	*Aureobasidium pullulans*	30.0c
Cladosporium herbarum	8.2c	Sterile dark 517	28.2cd
Aureobasidium pullulans	3.7c	Sterile dark 516	22.3cd
Sterile dark 516	2.0c	*Phoma* 445	17.3cd

mortality. There were no significant differences between the mortalities of either animal on any of the other fungal species. Feeding preference and mortality were not correlated for either *O. subtenuis* ($\varrho = -0.581$) or *O. nova* ($\varrho = -0.122$).

Discussion

Do O. subtenuis and O. nova have preferences for common litter fungi?

O. subtenuis and *O. nova* demonstrated definite preferences among common fungi. Evidence from a variety of studies on Collembola, oribatid mites, Enchytraeids and nematodes suggests that dematiaceous species are preferred to hyaline species (Addison 1977; Dash & Cragg 1972; Klironomos et al. 1992; Mitchell & Parkinson 1976; Visser & Whitakker 1977; Whitakker 1981). In other studies on Collembola and oribatid mites there is no clear preference of dematiaceous over hyaline fungi (Luxton 1972; McMillan 1976) and in the study by Mitchell & Parkinson (1976) though the data suggest a preference, there was no statistical analysis of this result. Although *O. subtenuis* and *O. nova* preferred dematiaceous species in the present experiment, very few hyaline species were offered, so it is difficult to determine if the preference for dematiaceous species holds. The evidence seems to be equivocal on this point in spite of the work by Klironomos et al. (1992) in vitro suggesting that faunal preferences for dematiaceous fungal species speeds up fungal succession.

Do these two animals prefer the same fungi?

O. subtenuis and *O. nova* do appear to distinguish between common litter fungi and do so in a similar manner such that their feeding preferences were not significantly different on needles. Since these two species are the dominant Collembola and oribatid mites in terms of numbers in Kananaskis lodgepole pine forests (Kaneko, unpubl. data), and they appear to prefer the same fungi, if they are active at the same time in the forest floor, one might expect that grazing by these species would have a significant impact on the litter fungal community. Other studies have indicated that Collembola may shift the competitive relationships between fungi colonizing litter (Newell 1984a, b; Parkinson et al. 1979) in microcosms and in the field. As potential competitor for fungal diet in the soil, both Collembola and oribatid mites should be studied when considering fungal grazing in the soil system.

That a Collembola and a mite have similar feeding preferences for fungi is interesting in view of the more diverse feeding habits of Collembola than mites and in view of the size differences between the two species (*O. subtenuis* adults are often more than 1 mm long and *O. nova* adults are approximately 0.26 mm long).

Do these preferences depend on whether the fungi are grown on agar or pine needles?

For *O. subtenuis* there was a significant difference in preference for fungi grown on agar and needles, for example, *Phoma* 445. *Folsomia candida* (Collembola) also showed changes in preference for fungal species depending on the substrate on which they were grown; *Trichoderma koningii* was a preferred food when grown on balsam fir litter and avoided when grown on either agar or Norway spruce litter (Klironomos et al. 1992). These changes may be due to differences in production of volatile compounds by fungi. Bengtsson et al. (1988) observed that the volatile compounds given off by three species of fungi differed when they were grown on agar and in soil and that the Collembola *Onychiurus armatus* responded differently to the fungi on these substrates. They also observed that although the gas chromatograms of *Penicillium spinulosum* and *Mortierella isabellina* when grown on soil were somewhat different, the Collembola did not distinguish between them, even though when offered as food, *M. isabellina* was significantly preferred (Bengtsson et al. 1988), indicating that both volatiles and taste are important cues for Collembola. Volatile compounds and amounts of these compounds produced by *Mortierella isabellina* differed when grown on agar or soil (Bengtsson et al. 1991).

Interestingly, *O. nova* did not respond differently to fungi grown on agar or needles. In spite of the fact that *O. nova* is significantly smaller than *O. subtenuis*, hyphal diameter did not appear to be a limiting factor for *O. nova*. McMillan (1976) and Schultz (1991) did not observe any relationship between size of hyphae or spores and feeding preference by a Collembola; fungi with similar structure were not grazed in a similar manner, and large as well as small spores were equally preferred.

Do the fungal food preferences correlate to the animal's survival on that fungus?

Our results are consistent with other studies showing that preference for fungi is a rough indicator of survival and reproductive success although Collembola and mites can survive and reproduce on a wide range of fungi (Addison 1977; Klironomos et al. 1992; Mitchell & Parkinson 1976). Amelsvoort et al. (1989) showed that life history parameters of *Folsomia candida* were affected by fungal food quality. Under favorable food conditions, *F. candida* maximized population growth through increased fecundity and growth and under less favorable food conditions, they produced fewer eggs and lived longer (Amelsvoort et al.

1989). Stefaniak and Seniczak (1981) examined the feeding preference and reproductive success of *Oppia nitens* when presented with 12 fungal species. They recognized four groups of these fungi; a) those on which active feeding and early sexual maturity occurred; b) those where many eggs were produced but there was poor feeding by juveniles and early mortality; c) those which were eaten reluctantly; and d) those on which there was no feeding and no egg production. There appears to be a wide range of fungi on which *O. subtenuis* and *O. nova* can survive although the fungi may not be highly preferred. This would be a useful strategy for small edaphic organisms living in a heterogeneous habitat where preferred fungi may be inaccessible.

O. subtenuis did appear to respond differently to fungi when grown on agar or needles, although *O. nova* did not. Given the evidence presented here, we recommend that feeding choice studies be conducted using natural substrates to best emulate field conditions.

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